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The Coexistence of Ecologically Similar Species

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The Coexistence of Ecologically Similar Species

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The biological diversity on planet Earth is astounding. Understanding the origins of this diversity, and how it is maintained, are the twin goals of ecology and evolutionary biology. An early and oft-repeated insight in this investigation is that that similar organisms cannot coexist indefinitely. Theory predicts that individuals and species will compete for limited resources and whichever has even a slight advantage will drive all others extinct in a process known as 'competitive exclusion'. By diversifying, species avoid competition, thereby 'stabilizing' their coexistence. Yet natural systems often display levels of diversity that are surprisingly high, given this theory and investigations of how the similarity of coexisting species is maintained have received much less attention. Using a combination of field studies and experiments I demonstrate that highly similar species of freshwater amphipods may compete for resources without resulting in competitive exclusion. These findings suggest that there exist a range of interactions among Hyalella amphipods, ranging from strong stabilizing effects due to ecological trade-offs, to weakly stabilizing effects, to a total lack of stabilizing effects among various pairs of species in this system. These findings demonstrate how the relative strength of stabilizing forces may vary among coexisting species.

Although much effort has been dedicated to enumerating and classifying the ways in which ecological and evolutionary forces promote diversity among species, there has been far less attention paid to mechanisms such as convergent evolution, habitat filtering, competition for non-substitutable resources, and non-ecological speciation, among others. I surveyed current theory that may explain the high levels of similarity among species often found in natural systems. I describe how several ecological and evolutionary mechanisms may operate to promote the coexistence of similar species and present results from new theoretical combinations of mechanisms to demonstrate how they may further act in concert with one another.

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Chapter 1: Niche overlap varies geographically in a complex of cryptic *Hyalella* amphipods

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ABSTRACT

The *Hyalella azteca* complex of freshwater amphipods is a striking example of cryptic species, where phenotypic similarity obscures truly non-interbreeding populations. We apply a new method to synthesize life history, habitat use, and morphological data to quantify the distinct niches of each species. Using survey data, we demonstrate that the coexistence of three *H. azteca* species is ubiquitous in Michigan lakes. Furthermore, we found differences in their within-lake microhabitat use. Each species appears to broadly prefer one of three microhabitat types: 1. extremely shallow nearshore waters; 2. the surface waters above macrophyte beds; and 3. the deep water within macrophyte beds. Intriguingly, these preferences vary across lakes, indicating that while habitat partitioning may play a role in maintaining coexistence in some lakes, in other lakes there is a high degree of habitat overlap. We expect that the niche differences, and lack thereof, that we describe among these *H. azteca* species will be characteristic of other cryptic species complexes.

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INTRODUCTION

The recent development of inexpensive and easy-to-use molecular tools has revealed that many previously described species are in fact collections of species with highly similar morphology (Bickford et al. 2007). These so-called 'cryptic species' appear to be a common phenomenon across taxonomic groups and biogeographic regions (Pfenninger and Schwenk 2007), and may be important components of biological diversity (Knowlton 1993, Sàez & Lozano 2005). In some cases they are isolated from each other geographically, but in many instances they can occur sympatrically (Witt and Hebert 2000, Alvarez *et al*. 2006). When cryptic species coexist with one another they may pose an intriguing challenge to ecological theory (Sàez and Lozano 2005, Siepielski and McPeek 2010), since species occupying the same ecological niche cannot coexist for long (Gause 1934, MacArthur and Levins 1967) but any real ecological differences between sympatric cryptic species may be subtle and potentially difficult to quantify.

Although the multidimensional nature of niches has been appreciated for some time (Hutchinson 1957) and many have sought to describe them along multiple axes using both categorical and continuous measures. However, there exist few methods for combining information from multiple sources into a single measure of niche overlap. A recently proposed statistical approach by Geange et al. (2011) allows for the integration of multiple data types (e.g. proportions, counts, continuous measures, etc.) and the calculation of a single overlap statistic that incorporates them all.

In this study, we determined the extent of niche overlap among three cryptic species of *H. azteca* amphipods found in Southern Michigan. Wellborn and Cothran (2007) examined a distance from shore gradient in one lake, a depth gradient in another (where one of the species was extremely rare), and compared fish stomach contents with field samples to assess predation risk. Here we apply a consistent sampling scheme to

each lake, across a wider spatial extent and range of lake sizes. We assessed whether previously reported microhabitat preferences are consistent across a representative set of 15 lakes. Using a method that can incorporate data from multiple niche axes (Geange et al. 2011), we then compared the relative niche overlap among all three species. Our findings indicate that one species occupies a different niche along multiple axes and we observe significant niche overlap between the other two species. Consistent with an integration of neutral and niche-based perspectives, we show that species pairs differ in their degree of niche differentiation, and this, in turn, may affect how strongly competitive outcomes are influenced by deterministic forces.

MATERIAL AND METHODS

Hyalella azteca species complex

An interesting example of cryptic species is the *Hyalella azteca* complex of freshwater amphipods. The genus *Hyalella* (Amphipoda: Hyalellidae) comprises 51 described species distributed throughout North, Central, and South America (Gonzalez and Watling 2002). One of these taxa, *H. azteca*, was formerly considered a single species and North America's most widespread invertebrate but genetic studies show that it forms a complex of >30 (mostly undescribed) species (McPeek and Wellborn 1998, Witt and Hebert 2000, Wellborn *et al*. 2005, Witt *et al*. 2006). Differences in some ecological traits, primarily body size and the presence of abdominal protuberances, have subsequently been identified in a few species. Several species of *Hyalella* are confined to a single watershed or lake and there are a few examples of endemic, highly divergent, locally-adapted species (Witt *et al*. 2006), for example *H. montezuma*, a planktonic filter-feeder found in a single fishless spring (Witt *et al*. 2003).

In temperate Midwestern North American lakes there are two easily distinguishable *Hyalella* types: a large morph and a small-bodied morph (Strong 1972, Wellborn 1995, Wellborn 2002). Large *Hyalella* are found in lakes with no fish or low levels of fish predation, while the small-bodied species seem to be exclusively found in lakes where fish are present. Experimental work and field studies suggest that the smaller *Hyalella* are competitively excluded from fishless lakes by their faster-growing, larger congeners but are able to evade predation and successfully establish dense populations in fish containing lakes (Wellborn 1994, Wellborn 2002). However, within each of these groups there are multiple species with poorly defined distributions and lacking reliable diagnostic differences in morphology, that are nonetheless genetically distinct and reproductively isolated from each other (Witt and Hebert 2000, Wellborn *et al*. 2005). In contrast with predictions of niche theory, assemblages of up to 4 cryptic *H. azteca* can coexist within single lakes while apparently exhibiting few ecological differences (Witt and Hebert 2000, Wellborn and Cothran 2004). Outside of the *H. azteca* complex, sympatric *Hyalella* species often show strong differences in traits and microhabitat use (e.g. *H. pleoacuta* and *H. castroi*, da Silva Castiglinoi and Bond-Buckup 2008). There may be similar, but much more subtle, differences in habitat use and vulnerability to predation among the cryptic co-occurring *Hyalella azteca* species, as suggested by Wellborn and Cothran (2007). Even so, documented differences remain subtle and these cryptic *H. azteca* still exhibit substantial overlap in their overall ecology.

Survey design

We surveyed 15 lakes across southern Michigan in June, 2007 (Figure 1). These lakes were distributed in two regions of southern Michigan: a western area near the Kellogg Biological Station (Kalamazoo county) and an eastern region near the Edwin S.

George Reserve Biological Station (Livingston county). All lakes were either known to contain fish based on prior work, or were confirmed as fish-containing lakes by successful trapping during the survey period. The three small-bodied cryptic *H. azteca* species previously collected from lakes in this region are as yet not formally described, and are referred to hereafter as "A", "B", and "C" (Wellborn and Cothran 2007, Dionne *et al*. 2011). Although all three species overlap in measures of body size, species B is on average slightly larger than species A and C (Wellborn and Cothran 2004). To determine whether the *H. azteca* species occupied different microhabitats, at each lake we sampled in three representative habitats previously suggested to be differentially used by these taxa (Wellborn and Cothran 2007): extremely shallow nearshore waters (0-0.2 m deep, 0-0.5 m from shore), shallow macrophyte beds near the surface of the lake (0-0.2 m deep, 1-5 m from shore), and deeper macrophyte beds extending to the lake bottom (1-1.5 m deep, 1-5 m from shore).

We collected amphipods in each habitat zone using fine-mesh (125-100 mm) dip nets. Each sweep of the net passed through approximately one liter of water containing macrophytes and other submerged debris, on and within which amphipods can be found. The number of sweeps performed ranged from 3 to 25, depending on the density of individuals present, with more sweeps conducted to ensure enough individuals would be obtained to determine the frequency of all three species. After each sweep, the contents of each sample was emptied into white plastic trays, sorted visually in situ, and all amphipods were transferred to plastic vials containing 95% ethanol using plastic pipettes. Samples were then frozen until further analyses.

Species identification

Due to their lack of distinguishing morphological differences, we identified each individual to species using a simple genetic analysis using polymerase chain reaction (PCR) developed by Wellborn and Cothran (2004). The PCR reactions use species-specific primers, which amplify a region of the COI mitochondrial gene and yield products that vary in length. Using the same forward primer (5'-acttctcttagagcgatta-3') and three reverse primers (species A: 5'-taagccgcttatcaaaagaa-3'; species B: 5'-taaaattgattgcccccaa-3'; and species C: 5'-gccccagctaaaacaggt-3') to produce PCR products of 260, 402, and 524 base pairs, respectively. We extracted DNA from whole individuals using a modified Chelex method (Walsh *et al*. 1991), amplified at an annealing temperature of 55 °C, and assessed PCR product length by agarose gel electrophoresis. All individuals recovered were genotyped (2480 amphipods; average *n* per lake ± SE = 165.3 ± 24.7 individuals), and we analyzed estimates of abundance as individuals/L assuming that each sweep captured all the amphipods in 1 L of habitat.

Statistical analyses of niche overlap

We followed Geange et al. (2011) in all of our niche overlap calculations. To compare habitat use across lakes we calculated niche overlap between species pairs within each lake considering the proportional use of each habitat (k from K = 3 categories) by each pair of species (i and j):

$$\mathrm{NO}_{ij} = \sum_{k=1}^{K} \min\left(p_{ik} p_{jk}\right)$$

This approach assumes that all habitats are equally available to each species. Although this assumption is certainly not true since there is far less nearshore habitat available within any given lake, we have scaled our counts according to our sampling effort since we lack detailed data on the relative abundance of each habitat type.

We calculated niche overlap for six other traits (head length, clutch size, egg volume, gnathopod size, spine length, and sex ratio) using data from previously-published studies (Wellborn 2000, Wellborn 2004) following the formulae provided by Geange et al. (2011) and their accompanying R code for randomization testing. In brief, to assess the significance of niche overlap, we randomly shuffled species identity for each measure and recalculated the pairwise overlap 10,000 times. The *p*-value for each comparison is the number of times the niche overlap from a randomization is lower than the actual value observed. Because of the large number of tests we applied a sequential Bonferroni correction (Gabaldón et al. 2013).

To describe variation in habitat use across lakes we also used a mixed effects analysis of variance (ANOVA) to test for a random lake effect, for effects of habitat type, species, and their interaction on density. Based on their morphology, we anticipated that species A and C would be most similar in their habitat use, while species B, the most morphologically distinct, would exhibit a different pattern from these other two. Thus, we focused our analysis of the survey and experimental results on two planned contrasts: first, comparing the ratio of the density of species B to the combined density of species A and C, and second, the ratio of the density of species A to species C. Both of these ratios were compared across habitats in mixed effects ANOVAs, with a random lake effect and habitat zone as a fixed effect. All analyses were executed in R (R Core Team 2012), using additional functions for mixed model analysis from the nlme (Pinheiro *et al*. 2012) and multcomp packages (Hothorn *et al*. 2008).

RESULTS

Hyalella azteca densities ranged from 0.64 to 80.5 individuals/L (mean density ± SE = 24.14 ± 13.65 individuals/L) and all three species were found in all lakes, with one

exception: species B was not found in Duck Lake West (Figure 1.1). Although species B has been previously recovered from this lake, it exists there at very low abundances (Wellborn and Cothran 2007) which may explain its absence from our surveys. All species were observed in all the within-lake habitats, in at least some lakes.

Species differed in their overall densities ($F_{2,103} = 9.615, p = 0.0001$), with species A being significantly more abundant than both species B ($p = 0.0018$) and species C ($p = 0.0475$). The three habitat zones had did not differ significantly in the density of *H. azteca* ($F_{2,103} = 2.190, p = 0.117$). There was a significant interaction between species and habitat zone, indicating differential habitat use by the three *H. azteca* species ($F_{4,103} = 2.572, p = 0.0422$). This was driven by a significant difference in the density of species B in the nearshore zone ($p = 0.0216$), while the density of species A and C responded similarly across habitats ($p_{\text{surface}} = 0.266, p_{\text{nearshore}} = 0.423$).

The ratio of species B to the combined density of species A and C differed across the habitat zones ($F_{2,25} = 6.683$, $p = 0.0047$, Fig. 2a.), but only marginally across lakes ($F_{14} = 2.002$, $p = 0.063$). This habitat effect was due to significant differences between the nearshore habitat and the other two zones (Tukey's HSD $p_{\text{nearshore vs. deep}} = 0.0071$, $p_{\text{nearshore vs. surface}} = 0.0029, p_{\text{deep vs. surface}} = 0.919$). In contrast, the density ratio of species A:C was consistent across the habitats ($F_{2,25} = 2.484$, $p = 0.104$, Tukey's HSD $p_{\text{nearshore vs. deep}} = 0.890, p_{\text{nearshore vs. surface}} = 0.085, p_{\text{deep vs. surface}} = 0.205$), Fig. 1.2b.).

The niche overlap analysis revealed that when multiple axes are considered simultaneously, we can identify differences among all three *Hyalella* species, despite broad overlap in nearly all traits (Table 1.1, Figure 1.3). This overlap is especially high between species A and species C, which makes their overlapping habitat use even more surprising. The niche overlap analysis detected an average pattern consistent with previous reports, of A preferring the surface waters, B in the nearshore, and C using the

deeper water within macrophyte beds. However, calculating niche overlap in habitat use for each lake revealed geographic variation in the patterns of use within different lakes (Table 1.2, Figure 1.4).

DISCUSSION

Our survey of cryptic *H. azteca* has revealed their co-occurrence to be ubiquitous. Only in a single lake did we fail to find one of the species. This lake, Duck Lake West, had the lowest average density of amphipods and with only 27 individuals recovered from this location, it is unsurprising that one of the species was not detected here. We found that species A and C were most similar in their patterns of habitat use: both were rarely found in the nearshore habitat, while species B *H. azteca* was most commonly observed in this zone. Although species A dominated numerically in nearly all lakes, evidence of habitat partitioning between species A and C was not universal across lakes. Thus, while there is divergence between A and C in their use of habitats these patterns are not consistent across lakes. This was in contrast to our finding that species B appears to specialize on the nearshore habitat. The divergence in habitat use between species B and the other two *H. azteca* is consistent with previous work conducted in a smaller number of Michigan lakes (Wellborn and Cothran 2007). Species B is, on average, larger than species A and species C, and their larger body size appears to increase their vulnerability to fish predators (Wellborn and Broughton 2008, Wellborn and Cothran 2007). This may explain their preference for the nearshore habitat, which is so shallow as to exclude most fish, especially the dominant predators in this system (mainly *Lepomis spp*. sunfish).

The body size and life history differences between the different *Hyalella* species are genetically based, not merely plastic responses (Wellborn 2002). Molecular

phylogenetic analyses of *Hyalella* lineages have revealed parallel evolution of similarly sized morphs, likely in response to strong selection by predators, and independent evolution of the small-bodied morph in different regions (Wellborn and Broughton 2008). Adaptation to avoid predation has driven many species of *Hyalella* to converge on an extremely small body size, apparently without generating any other gross differences in morphology. Speciation does not necessarily imply the evolution of ecological differentiation, and several examples of diversification without niche shifts have been recorded (e.g. via the evolution of mate-recognition systems (Ritchie 2007) or isolation by chromosomal inversions (Noor *et al*. 2001), *inter alia*). Recent theoretical work suggests that niche differentiation may even help push subsets of species to converge on the same ecological optima, resulting in the kind of equivalence necessary for neutral coexistence (TerHorst *et al*. 2010). When faced with uniform natural selection, e.g. preferential predation on larger individuals, populations should respond similarly in terms of adaptation and simultaneously become differentiated in traits uncorrelated with fitness (Bell 2013), since traits not directly under selection should be free to vary. Species assemblages that have radiated by these and other mechanisms may be productive avenues of investigation for other examples of the kind of weak ecological differentiation examined here, allowing us to assess just how different species niches need to be for stable coexistence to occur.

The hidden potential of cryptic species

Biological diversity is generated and maintained by mechanisms that allow individuals to minimize interspecific competition (Chesson 2000). There has been substantial debate over whether neutral or niche models better explain patterns of biodiversity (e.g. Leibold and McPeek 2006, Adler *et al*. 2007), however, the bulk of this

work has focused on fitting species abundance distributions (Bell 2001, Hubbell 2001). This is a poor diagnostic since both types of models are capable of producing a wide variety of abundance distribution patterns (Chave 2004). Moreover, we still do not know if any naturally coexisting species are similar enough in their ecology for neutral dynamics to occur (but see Chave 2004, Bell *et al*. 2006, McGill *et al*. 2006). Truly neutral species may arise via parallel evolution in sympatry or through divergence not associated with ecological differentiation, for example through changes in mate recognition systems (McPeek and Gomulkiewicz 2005, Holt 2006). Many species may be similar enough for their coexistence to depend on equalizing (neutral) forces rather than stabilizing (niche-based) ones. However, when niche differences are small, only small differences in competitive ability are required to drive competitive exclusion (Chesson 2000, Mayfield and Levine 2010). While one might expect the stochastic extinction of neutral, ecologically equivalent species to have occurred in at least some of the lakes surveyed, it is important to keep in mind the very high densities of *Hyalella* these lakes contain. With population sizes estimated between 10^5 and 10^8 individuals, depending on the size of the lake and its littoral zone (Wellborn 1992, McPeek and Gomulkiewicz 2005), the rate at which species may drift to extinction will be greatly delayed (Hubbell 2001, McPeek and Gomulkiewicz 2005).

In the current system, other investigators have documented substantial niche overlap and a lack of differentiation for nearly every aspect of *H. azteca*'s ecological niche that has been examined. Dionne et al. (2011) found no differences in the temporal turnover of three *H. azteca* species, suggesting a lack of seasonal differences in their demographics and response to the environment. Wellborn and Cothran (2004) documented overlap between species A and C in nearly every aspect of morphology they measured, including male and female body size, clutch size, egg volume, male gnathopod

size, and patterns of sexual size dimorphism. There may yet nonetheless exist differences among these species along some as-yet unmeasured axis of niche space. Although we cannot entirely rule out this alternative explanation, we consider it unlikely in the case of *H. azteca* amphipods.

It seems unlikely that real species will ever be exact ecological equivalents (McPeek and Gomulkiewicz 2005, Leibold and McPeek 2006). However, if ecologically similar species are common in nature, ecological drift may be a common phenomenon. Groups of cryptic species are perhaps most likely to show equivalence in the sense assumed by neutral models of community assembly (McPeek and Gomulkiewicz 2005, Alvarez et al. 2006). We suspect that the niche differences (or lack thereof) we can detect between species like A and C *H. azteca* will be characteristic of other pairs of cryptic species. Furthermore, measurable differences between co-occurring species pairs do not necessarily imply that niche differences are stabilizing coexistence (Siepielski and McPeek 2010). Further studies of *H. azteca* that test for frequency-dependence will serve as a strong test of whether cryptic species may behave as functionally neutral species in a community despite any subtle niche differentiation. While cryptic species may be a special case, the argument over the relative strength of diversifying niche selection and selection imposed by a shared environment is also relevant for any species that share ecological properties (e.g. members of guilds or functional groups; Case and Taper 2000).

Nested neutral and niche-based dynamics

Neutral coexistence and niche differentiation are unlikely to operate in total isolation, but rather, probably in a nested set of species assemblages. For example, damselflies in the genera *Ischnura* and *Enallagma* clearly trade-off predator avoidance

and energy conversion efficiency to occupy separate niches and locally coexist in lakes throughout North America (McPeek 1998). However, within each genus there are consistently multiple species found in the same lake. A combination of field surveys and enclosure experiments has demonstrated that (for the *Enallagma* species at least) interactions within the genus are approximately neutral (Siepielski *et al*. 2010).

Previous work has demonstrated strong niche differentiation between the large and small bodied *Hyalella* species of North America. Our findings suggest that there exist a variety of competitive interactions among *Hyalella* amphipods, including the subtle differences in habitat use and predator vulnerability between species B and the other small-bodied taxa, to the weak differentiation observed between species A and C. Thus, while some *Hyalella* are known to trade-off predator types (large species in fishless lakes, and small species in lakes with invertebrate predators) the minor differences we observed between species A and C may not be sufficiently strong to shape their distribution patterns within or across lakes suggesting a strong role for stochastic forces instead (see Siepielski and McPeek's 2010 critique of the coexistence program). At what point are species similar enough, even if they show some niche differentiation, that stochastic processes of demography and migration become more important than any such frequency dependence? If ecologically similar species are common in nature, it will be imperative to understand the dynamics of neutral or nearly neutral interactions, and systems such as cryptic *Hyalella* are a good place to start.

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TABLES

Table 1.1. Results of multidimensional niche overlap analysis.

For each niche axis, we report the overlap observed between each species pair. Values that indicate significant niche differentiation are indicated in bold (those that remained significant after a Bonferroni correction are indicated with an asterisk).

Niche axis	A and B	B and C	A and C
Habitat use	**0.61***	**0.54***	**0.92***
Head length	**0.63***	**0.61**	0.96
Clutch size	0.96	0.99	0.96
Egg volume	0.71	0.55	0.81
Sex ratio	**0.85***	**0.92**	0.93
Gnathopod length	**0.46***	**0.30***	**0.73***
Spine length	**0.43**	**0.36***	**0.66***

Table 1.2. Results of within-lake niche overlap analysis.

For 14 lakes we were able to compare the overlap in habitat use between each species pair. Note that all species pairs demonstrate high overlap in some lakes and that the highest average overlap is observed between species A and C. Lastly, the proportion of lakes where we observed significant differences in habitat use was lowest when comparing species A and C.

	A and B	B and C	A and C
Lowest overlap observed	0.18	0.00	0.25
Highest overlap observed	0.83	0.95	0.94
Average niche overlap	0.52	0.46	0.65
Proportion of lakes with significant habitat use differences	0.42	0.57	0.29

FIGURES

Figure 1.1. The spatial distribution of cryptic *Hyalella azteca* in southern Michigan, June, 2007.

Map on left indicates region of Michigan surveyed. Pie diagrams on the right indicate the relative abundance of the three cryptic *H. azteca* species found at each lake.

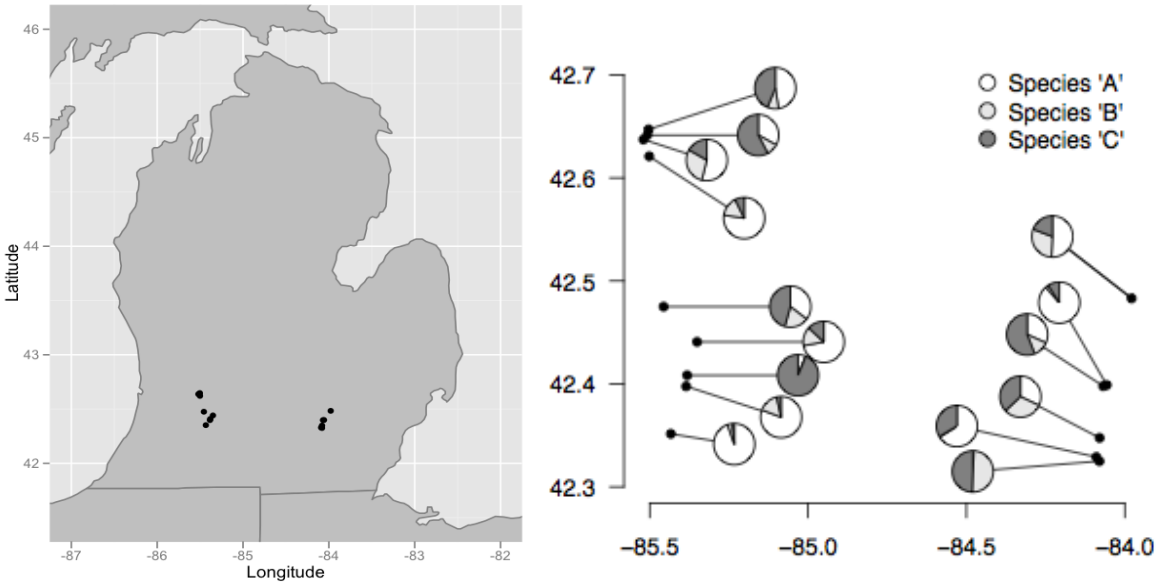


Figure 1.2. Relative abundance patterns of cryptic *Hyalella azteca* across lake microhabitats.

A) The mean ratio of *Hyalella azteca* B's density to the combined density of *H. azteca* A and C in the deep, surface, and nearshore habitat zones. **B)** The mean ratio of *H. azteca* A's density to the density of *H. azteca* across the deep, surface, and nearshore habitat zones. Error bars represent 95% confidence intervals and statistically significant means (based on Tukey's HSD analysis) are indicated by different letters.

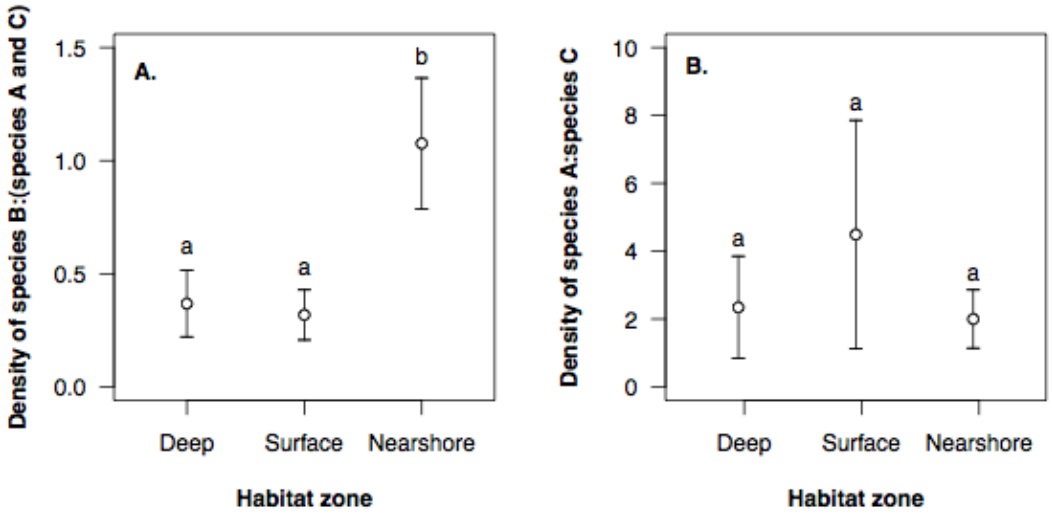
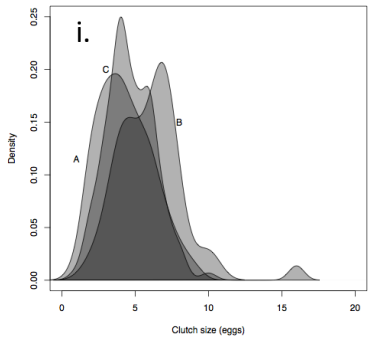
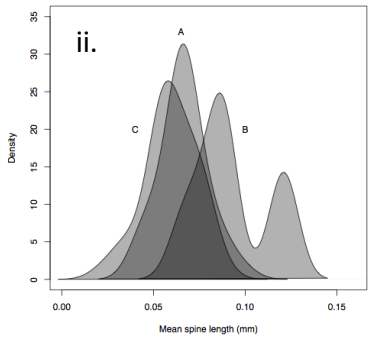


Figure 1.3. Trait distributions illustrate niche overlap and differentiation between species pairs.

Three examples are presented to illustrate i) overlap among all three species in clutch size; ii) differentiation among all species in spine length; and iii) overlap between species A and C, but divergence of species B in head length.





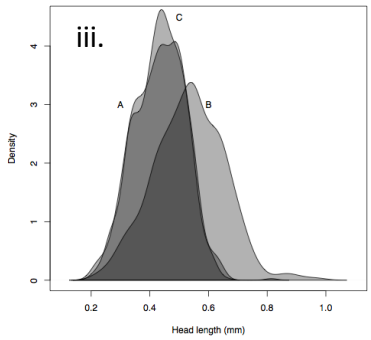
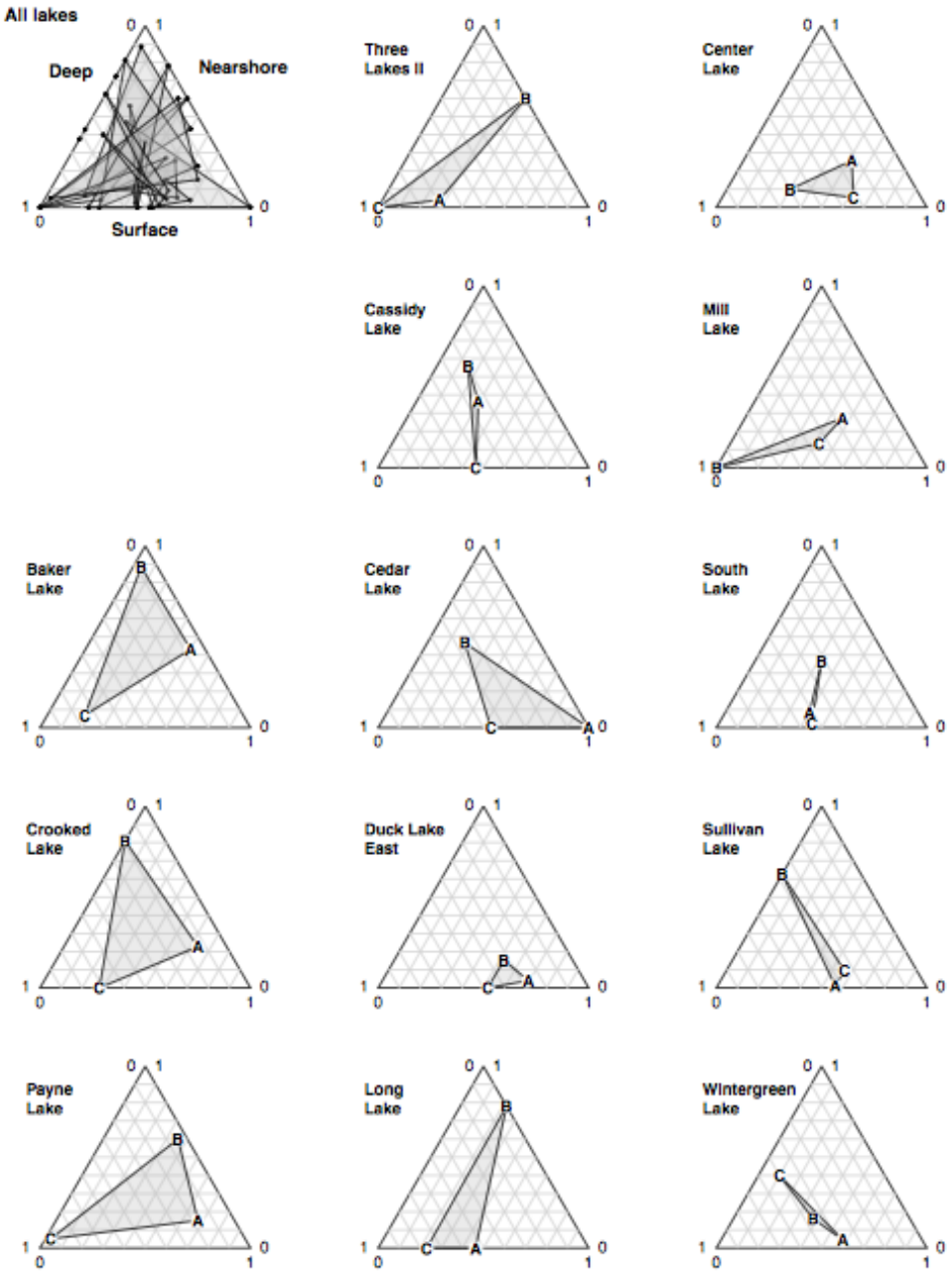


Figure 1.4. Niche occupancy across lakes.

To illustrate differences in habitat occupancy across lakes, we plot the proportional habitat use for each species and link them with a shaded triangle. The top left plot includes all lakes. The five plots in the right-hand column indicate lakes where we observed deviations from the standard hierarchy of B in the nearshore, A in the surface, and C in the deep habitat.



Chapter 2: Experimental evidence for niche equivalence and differentiation within a cryptic species complex

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Statement of Authorship: All authors contributed to the design of the experiment. G.K.S. performed the experiment, performed the analyses, and wrote the manuscript. All authors discussed the results and commented on the manuscript.

ABSTRACT

Niche differences need not prohibit the occurrence of neutral interactions among species. Likewise, no natural community is strictly governed by ecological drift. Using field-collected populations in outdoor mesocosms, we evaluated the relative contribution of niche and neutral dynamics in a group of commonly co-occurring cryptic amphipod species in the genus *Hyalella*. Targeting habitat partitioning and differential predation vulnerability, we tracked the outcome of competition between a larger-bodied *H. azteca* species and three smaller unnamed cryptic species, referred to throughout as 'A', 'B', and 'C'. While we found strong evidence for niche differentiation among some species (between large and small, and between B and the other two small species), we did not observe any niche differences between two of the cryptic species, A and C. Our findings indicate that a range of competitive interactions exist among *H. azteca* amphipods; while some pairs show strong ecological trade-offs, others show weak or no differences.

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INTRODUCTION

Neutral coexistence theory presumes ecological equivalence among competing species and posits that such equivalent species can co-occur for extended periods of time as their relative abundances change via a completely stochastic drift process (Bell 2001, Hubbell 2001). The suggestion that niche differences play no role in determining large-scale patterns of the distribution and abundance of species has stimulated vigorous debate among community ecologists (Clark and McLachlan 2003, Chave 2004, McGill et al. 2006, Leibold and McPeek 2006). However, to date, the debate between advocates of neutral dynamics and those favoring niche differentiation has focused on how well either type of model explains a handful of observable large-scale patterns in natural communities. There have been very few direct tests of the relative importance of niche-based and neutral dynamics in determining the structure of local communities (but see Siepielski et al. 2010).

There are two diagnostic features that can be used to detect niche partitioning in species interactions. First, species should exhibit negatively frequency-dependent per capita growth rates, with higher values when their relative abundances are low and they experience reduced intra-specific competition. In other words, they should demonstrate an advantage when rare. This type of evidence may be achieved using experiments where the relative abundance of competitors is manipulated (e.g. Siepielski et al. 2010), which may prove challenging in some systems. Second, species may display context-dependence, i.e. their per capita growth rates or the outcome of competition should depend on the availability of the particular niche space they occupy (e.g. Wellborn 2002). This approach is also limited, in that it relies on the ability of the researcher to determine the appropriate axes of niche space to manipulate. While most studies look for the presence and/or absence of niche and neutral dynamics in entire communities, studies

testing for frequency-dependence and/or context dependence ask a more subtle question. Specifically, they are concerned with whether drift dynamics among subsets of species are important. The potential importance of neutral, or near neutral, dynamics in communities will depend on how frequently communities contain species with very close ecological similarity. We suggest that such groups of species may be much more common than is generally appreciated. We test here the relative role of niche and neutral dynamics by testing for context-dependence using a group of species likely to exhibit a range of interactions.

With the rapidly declining costs of molecular sequencing tools, biologists have discovered that many groups of organisms that were once considered single species are in fact collections of multiple species that do not interbreed. In cases where this diversity is not reflected in any morphological variation among species, the term 'cryptic species' is often applied. Closer examination of cryptic species has found that in many instances they occupy spatially segregated ranges or distinct ecological niches. For example, the freshwater invertebrate *Hyalella azteca* was once thought to be a single species with a distribution spanning all of North America. But several decades of molecular work and detailed field surveys have revealed that *H. azteca* is a cryptic species complex, comprising at least 30 species (McPeek & Wellborn 1998, Witt & Hebert 2000, Wellborn et al. 2005, Witt et al. 2006). Some of these *H. azteca* have evolved ecological specializations that allow them to locally co-occur with other *H. azteca*. Researchers have documented several cases where morphologically distinct populations of *H. azteca* co-occur with no individuals of intermediate morphologies, suggesting a lack of hybridization between the two. Many of these have subsequently been described as new species (e.g. *H. montezuma*, Stevensen and Peden 1973, Witt et al. 2003, and *H. texana*, Cole and Watkins 1977). In other cases, highly similar species of *H. azteca* occupy

restricted, non-overlapping ranges. In the Great Basin region of California, Nevada, and Utah, typically only single lineages of *H. azteca* are found in the same site (Witt et al. 2008). Ecological divergence and non-overlapping ranges of similar species are outcomes consistent with predications regarding cryptic species. In a niche dynamics model, similar species shouldn't be able to coexist locally, they should displace each other either ecologically or geographically.

Within the *H. azteca* complex there are a two sets of species that have diverged in overall body size, while retaining highly similar gross morphology, referred to as "large" and "small" *H. azteca* (Strong 1972, Wellborn 1995, Wellborn 2002). Large *H. azteca* are on average approximately 1.5 times larger than any of the small species (Wellborn 2002, Wellborn and Broughton 2008). Their size differences result in differences in competitive ability and in their vulnerability to fish and invertebrate predators. Large *H. azteca* are more vulnerable to fish predation and thus are found only in fishless lakes, while small *H. azteca*, which can more easily avoid predation by fish, occupy fish-containing lakes where they are consumed by invertebrate predators (mainly dragonfly larvae). Thus, while they occupy broadly overlapping spatial distributions, they have partitioned the lakes within their ranges based largely on the presence or absence of fish. Experimental work and field studies suggest that the smaller *Hyalella* are competitively excluded from fishless lakes by their faster-growing, larger congeners but are able to evade predation and successfully establish dense populations in fish containing lakes (Wellborn 1994, Wellborn 2002).

However, there is even more diversity lurking in the *H. azteca* cryptic complex. Fish-containing lakes appear to house as many as four cryptic species of small-bodied *H. azteca* (Witt and Hebert 2000). Three species consistently co-occur in the lakes of central Michigan (Wellborn and Cothran 2007, Smith et al. in review). The three cryptic *H.*

azteca species in this region are as yet not officially described, and are referred to hereafter as "A", "B", and "C" (Wellborn & Cothran 2007, Dionne et al. 2011). Detailed field surveys indicate that they may be partitioning within-lake habitats and that perhaps the same forces that have shaped the distributions of the more-obviously differentiated *H. azteca* are also acting at this smaller scale (Wellborn and Cothran 2007, Smith et al. in review). One of the three small *H. azteca* species (named "B") is slightly larger than the others, and it appears to prefer predator-free areas very close to shore. There is little evidence of any niche partitioning between the remaining two small *H. azteca* species (named "A" and "C") that are common in this system (Wellborn and Cothran 2007, Smith et al. in review) and we consider A and C to be the most likely to exhibit neutral interactions.

We set up replicate mesocosms to measure the degree to which niche partitioning among habitats contributes to the maintenance of diversity in this system. By manipulating predation and environment, we compared the role played by habitat partitioning (i.e. niche dynamics) between large and small *H. azteca* to its contribution to the dynamics of the smaller species. Our expectation was that niche dynamics would be important between large and small *Hyalella*, but drift (i.e. neutral dynamics) would predominate among small *Hyalella*. We found that there were strong effects of fish predators on the outcome of competition between large and small *H. azteca,* but this effect was weak among the small *H. azteca*. We show that species pairs in the *H. azteca* complex differ in their degree of niche differentiation, and that these differences, in turn, affect how strongly competitive outcomes are influenced by deterministic forces.

MATERIAL AND METHODS

Mesocosm experimental design

We established our experimental mesocosms at the W.K. Kellogg Biological Station Pond Lab, Hickory Corners, Michigan, using commercial sand, well water, and chemical nutrient additions. To provide a food source for the amphipods we added a concentrated mix of local phyto- and zooplankton species from nearby lakes, and let these communities establish for 10 days before introducing any *H. azteca* individuals. We collected small-bodied *H. azteca* from Payne Lake (42.6471˚N, 85.5035˚W), where we had observed high densities of all three species. To ensure that we collected individuals of all three species, we collected amphipods in each habitat zone using small, fine-mesh (125-100mm) dip nets. Each sweep of the net passed through approximately one liter of water containing macrophytes and other submerged debris, on and within which amphipods can be found. We reserved a subsample from these individuals and confirmed that all three were present in the stock added to the experimental tanks. Large *H. azteca* were obtained from a small fishless pond on the K.B.S. Pond Lab grounds.

Previous work has established that among the small species, B strongly prefers shallow, nearshore habitat, while species A and C prefer the surface and deep macrophyte beds, respectively (Wellborn and Cothran 2007, Smith et al. in review). Thus, replicate mesocosms were set up with the following conditions: 1. mesocosms lacking any shallow, nearshore habitat (by placing these tanks on a flat surface), 2. mesocosms lacking a surface macrophyte bed, 3. mesocosms lacking a deep macrophyte bed, and 4. control mesocosms with all three habitat types available. In tanks where a given habitat type was missing (conditions 1-3) both other types were still available. We mimicked natural macrophyte beds using frayed lengths of polystyrene ropes affixed to poles, allowing us to set the “beds” at specific heights (deep or at the surface). To create a

shallow "nearshore" habitat we placed tanks on a slope of approximately 15 degrees (Figure 2.1). Anticipating that the importance of habitat availability may depend on the presence of fish predators, we established two predation levels by adding fish to half of the tanks. Tanks without fish were covered with mesh lids to prevent colonization by invertebrate predators.

All mesocosms were destructively sampled at the end of 5 weeks (approximately 1.5-2 generations for *H. azteca*) and all individuals were preserved in alcohol for genetic identification. Due to their lack of distinguishing morphological differences, we identified each individual to species using a simple genetic analysis using polymerase chain reaction (PCR) developed by Wellborn and Cothran (2004). The PCR reactions use species-specific primers that amplify a region of the COI mitochondrial gene and yield products that vary in length. Using the same forward primer (5'-acttctcttagagcgatta-3') and three reverse primers (species A: 5'-taagccgcttatcaaaagaa-3'; species B: 5'-taaaattgattgcccccaa-3'; and species C: 5'-gccccagctaaaacaggt-3') to produce PCR products of 260, 402, and 524 bp, respectively. We extracted DNA from whole individuals using a modified Chelex method (Walsh et al. 1991), amplified at an annealing temperature of 55 °C, and assessed PCR product length by agarose gel electrophoresis.

Statistical analyses

We compared the proportion of small *H. azteca* individuals in tanks with and without fish predators using a t-test and a non-parametric Wilcoxon rank sum test. To compare how species B responded to our habitat availability treatments, we used a two-way ANOVA, including the presence/absence of the nearshore habitat and the presence/absence of fish as fixed explanatory factors. To compare how the relative abundance of species A and C varied, compared the proportion of A and C individuals

represented by species A across all tanks, using experimental treatment and the presence of fish as factors in a two-way ANOVA. All analyses were executed in R (R Core Team 2012).

RESULTS

Species A had a numerical advantage over species B and C at the start of the experiment. It comprised approximately 71.3% (±3.66% SE) of the small *H. azteca* individuals used to seed the tanks, while species B represented only 8.78% (± 3.72%) and species C represented 19.9% (±7.39%). This reflects the natural variation in overall densities of the small *H. azteca*, which is relatively consistent across lakes in this region (Smith et al. in review).

In competition experiments among all four *H. azteca* species, the presence of fish predators had a significant positive effect on the proportion of small-bodied *H. azteca* in mesocosms with both size morphs (Figure 2.2.A, Student's *t*-test *p*-value = 0.01, Wilcoxon rank sum test *p*-value = 0.02). This was consistent with our expectation that large-bodied *H. azteca* would suffer disproportionately from fish predation, as seen in previous experiments (Wellborn 2002).

In competition experiments using only the three small-bodied *H. azteca* species, we found that the availability of the nearshore habitat had a significant effect on the proportion of individuals represented by species B, depending on whether or not fish predators were present (Figure 2.2.B, Table 1, significant interaction term: $p\text{-value}_{\text{nearshore} * \text{fish}} = 0.01$). In the presence of fish the abundance of species B was reduced when the nearshore habitat was unavailable. This was as expected, given that species B is slightly larger than species A and C, and therefore more vulnerable to fish predation in the absence of the shallow, nearshore habitat it prefers in the wild. There were no significant

main effects detected (Table 2.1), reflecting the increase in the relative abundance of species B in the remaining tanks when fish were absent. This suggests that species B exhibits some kind of trade-off between competitive ability and predator avoidance (Figure 2.2.B). While species A had a numerical advantage over species C in nearly all the tanks, stemming from its higher abundance in our field collections, there were no significant differences in their relative abundances across the treatment groups, or between fishless and fish-containing tanks (Table 2.2, Figure 2.2.C).

DISCUSSION

In our mesocosms, the outcome of competition between large and small *Hyalella azteca* depended on the presence of fish predators. This confirms the findings of previous experiments and field studies documenting a trade-off between vulnerability to fish predation and competitive ability (Wellborn 1994, Wellborn 2002). Our experimental results suggest that a similar predator-avoidance/competitive ability trade-off exists between species B and the other small *H. azteca* species. Furthermore, the availability of the nearshore habitat is crucial for mediating the coexistence of species B with the other small-bodied *H. azteca* species, while we found no evidence of a similar role for habitat partitioning in the dynamics between species A and C. These findings suggest that there exist a variety of competitive interactions among *H. azteca* amphipods, ranging from the strong and obvious niche differentiation between the large and small bodied species, to the subtle differences in habitat use and predator vulnerability between species B and the other small-bodied taxa, to the weak differentiation observed between species A and C. Thus, while some *H. azteca* are known to trade-off predator types (large species in fishless lakes, and small species in lakes with invertebrate predators) the minor differences in abundance between species A and C explained by habitat differences may

not be sufficiently strong to shape their distribution patterns within or across lakes. This lack of differentiation suggesting a strong role for stochastic forces instead (Smith et al. in review, Siepielski & McPeek 2010).

The fact that these *Hyalella* and many other 'cryptic species' often coexist even at a local scale provides one of the most illuminating ways to study the joint action of neutral and niche based coexistence mechanisms in nature. Cryptic species are sufficiently similar in morphology, behavior, and ecology that they are indistinguishable, save for when molecular tools are employed (Bickford *et al*. 2007). Cryptic species may comprise a great deal of unknown biological diversity, as they have been identified across nearly all parts of the globe and taxonomic groups (Knowlton 1993, Saez & Lozano 2005, Pfenninger & Schwenk 2007). When cryptic species are detected, they are sometimes subsequently found to occupy restricted, non-overlapping ranges, or distinct ecological niches (Alvarez et al. 2006, Witt et al. 2006). However, in other instances the local coexistence of cryptic species, with their extreme similarities, challenges traditional explanations for the maintenance of diversity via spatial or niche-based segregation (Sàez & Lozano 2005, Siepielski & McPeek 2010).

Groups of cryptic species are good candidates for the kind of strict ecological equivalence assumed by neutral models (McPeek & Gomulkiewicz 2005, Alvarez et al. 2006). Although it is possible that species A and C *H. azteca* are simply partitioning another niche axis in their environment, it is unclear what such an axis might be. Dionne et al. (2011) looked for, but found no evidence of temporal niche partitioning in a survey of small *H. azteca* across lakes in southeastern Québec. Wellborn and Cothran (2007) found that species A was the least vulnerable to predation and preferentially occupied the surface habitat of two lakes. However, Smith et al. (in review), in an expanded survey, found no consistent depth differences between species A and C. Ecological differences

between sympatric cryptic species may be subtle and escape investigation, but measurable ecological differences do not, on their own, constitute proof that niche differentiation is responsible for the coexistence of local competitors (Siepielski & McPeek 2010).

The neutral and niche-based perspectives on coexistence of similar species are often viewed as incompatible with one another. However, this dichotomous view of coexistence is not necessary and there is an emerging consensus that many communities are likely to be structured by both effects to some degree (Holt 2006, Gravel et al. 2006, Leibold & McPeek 2006, Cadotte 2007). In part this is because different perspectives may explain coexistence of different combinations of species, but also because niche similarity plays an important role in community assembly under the niche perspective due to 'fitness equalizing' components that may or may not relate to 'fitness stabilizing' components (Chesson 2000, Leibold 1998). In addition, evolutionary processes can in some circumstances lead to niche convergence resulting in equivalence (Scheffer & Van Nes 2006, Leibold & McPeek 2006, Holt 2006, terHorst et al. 2010). Unequivocal evidence for either mechanism in nature is sparse and debates have concentrated instead on the two perspective's abilities to explain distributional data without considering how they might jointly act to affect distributions.

Furthermore most of the work in this area has focused on entire assemblages, consisting of many species, rather than targeting species combinations most likely to show equivalence (but see Uriarte 2004, Wootton 2005, and Turnbull 2005). Thus it is possible that rejection of neutral models for entire communities may lead us to ignore the role of neutral dynamics involving small subsets of species (perhaps of those species that are most similar). It is our view that careful detailed work needs to be done to establish if neutral dynamics are important for subsets of species similar to each other, rather than for

entire assemblages of more heterogeneous groups of species. Experiments designed to detect signatures of neutrality have rarely been applied in the study the coexistence of species with overlapping ranges and niches (but see Siepielski et al. 2010), but our experiment does that by specifically targeting organisms most likely to exhibit neutral interactions. Demonstrating a lack of density-dependence in the *H. azteca* system would require being able to manipulate the abundances of each species, which is made difficult by their morphological similarities. However, there appear to be some subtle yet consistent color differences between the three small species used in this experiment (R. Cothran personal communication), which could be used for such work in the future. Approximately neutral dynamics between sub-groups of competitive communities, operating in conjunction with niche-based competition trade-offs, as suggested by the present study and work by Siepielski et al. (2010) is more likely than strictly neutral community dynamics, or strictly niche-based dynamics. We should perhaps target our investigations of neutrality not at the level of whole communities – where similar patterns of abundance structure may be generated by a variety of mechanisms – but instead at the level of particular sub-groups of species along a gradient of ecological similarity. Then, perhaps, we will begin to appreciate the role that ecological drift may play in structuring competitive communities.

We found that within a co-occurring assemblage of four cryptic species both niche and neutral processes are maintaining diversity. Our mesocosm experiments revealed that predatory fish determine the relative abundances of large and small *H. azteca*, and, in combination with habitat availability, drive abundance differences between small species B *H. azteca* and small species A and C *H. azteca*. Yet we did not discover any evidence for fitness stabilizing effects between small species A and C *H.*

azteca which suggests that neutral or nearly neutral processes are responsible for their patterns of relative abundance.

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TABLES

Table 2.1. Analysis of Variance Table comparing the response of species B *Hyalella azteca* across treatments with, and without, the nearshore habitat and the addition of fish predators.

	Degrees of freedom	Sum of squares	Mean squares	*F*-value	*P*-value
Nearshore habitat	1	0.0005	0.0005	0.187	0.6686
Fish	1	0.0017	0.0017	0.6726	0.4202
Nearshore habitat * fish	1	0.0193	0.0193	7.6050	**0.0110**
Residual	24	0.0623	0.0026		

Table 2.2. Analysis of Variance table comparing the effects of habitat removal in the presence, and absence, of fish predators on the proportion of species A and species C *Hyalella azteca* individuals represented by species A.

	Degrees of freedom	Sum of squares	Mean squares	F-value	P-value
Habitat treatment	3	0.1588	0.0529	0.7378	0.5418
Fish	1	0.0073	0.0973	1.3567	0.2578
Habitat treatment * fish	3	0.1237	0.0412	0.5748	0.6382
Residual	20	1.4345	0.0717		

FIGURES

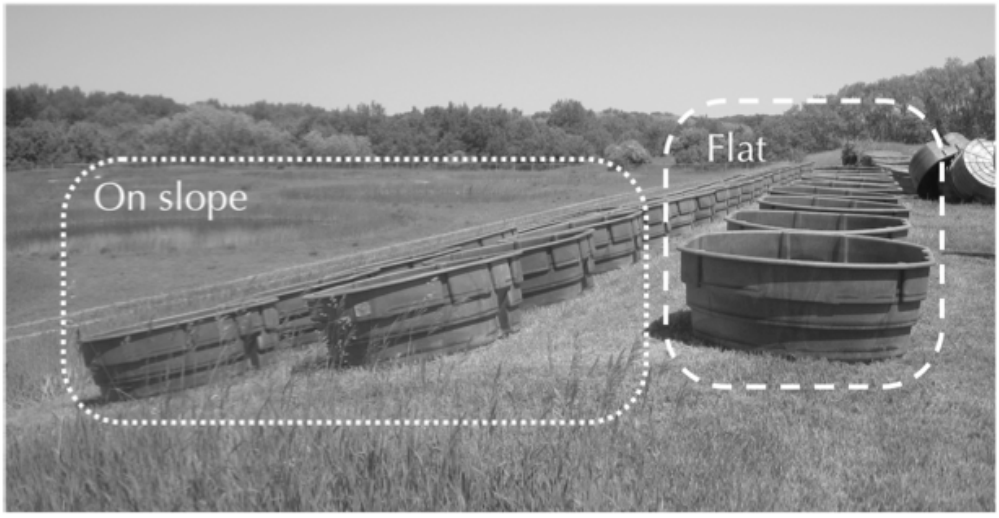

Figure 2.1. Experimental tank setup on the grounds of the W. K. Kellogg Biological Station, Hickory Corners, Michigan.

Tanks on the slope were randomly assigned to the Control, Deep removal, and Surface removal treatments. Tanks on the flat surface were used for the Nearshore habitat removal treatments.

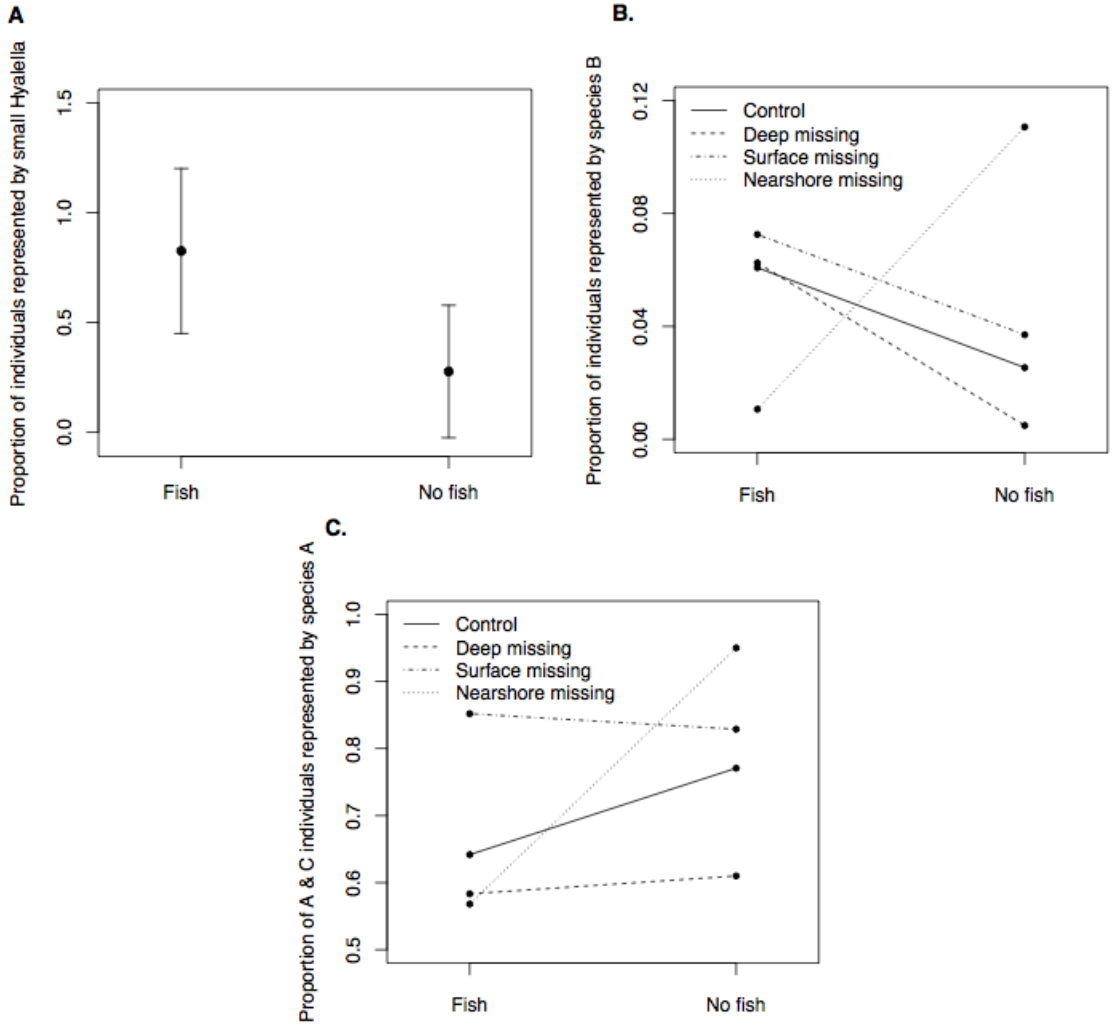

Figure 2.2. Competition mesocosm outcomes.

A. The effect of fish predators on the proportion of all *Hyalella azteca* individuals represented by small-bodied taxa. The proportion of small *H. azteca* is higher in tanks with fish predators, where the large-bodied individuals are predated upon selectively. **B.** The effects of fish predators and habitat removal treatments on the proportion of small *H. azteca* individuals represented by species B individuals in tanks with and without fish in tanks where the shallow, nearshore habitat zone was absent and in the remaining treatment groups. **C.** The effects of fish predation and habitat removal treatments on the relative abundances of species A and species C *H. azteca*.

Chapter 3. The ecological and evolutionary mechanisms that promote similarity among co-occurring species

Geneviève K. Smith[6]

INTRODUCTION

The organisms that inhabit planet Earth exhibit spectacular diversity, in form, function, and behavior. Understanding where this diversity comes from, and how it is maintained, are the twin goals of ecology and evolutionary biology. An early and oft-repeated insight in this investigation is that that similar organisms cannot coexist indefinitely (Hardin 1960). Theory predicts that individuals and species will compete for limited resources and whichever has even a slight advantage will deterministically overtake the other (Gause 1934, Hardin 1960). Ecological niche theory specifies formal conditions under which any species that becomes too rare will have an advantage over its competitors and increase in relative abundance thus regulating community structure patterns of coexistence and abundance (MacArthur and Levins 1968, Tilman 1982, Chase and Leibold 2003). Ecological communities are therefore predicted to comprise species with non-overlapping niches and there should be a limit to the similarity of coexisting species (MacArthur and Levins 1967, Chesson 2000, Chase and Leibold 2003). Similarly, in evolutionary models, competition for resources drives diversifying selection, favoring species with fewer competitors and resulting in character displacement or adaptive radiations (Brown and Wilson 1956, Schluter 1994). In fact, many of the most well known examples of evolutionary diversification, including character displacement and adaptive radiations (e.g. Darwin's finches, cichlids, honeycreepers), are believed to have been driven at least partly by selection for reduced competition (Schluter 2000). In

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sum, biological diversity is largely thought to be generated and maintained by mechanisms that allow individuals to avoid competition (Chesson 2000).

Despite the many examples and theory suggesting the importance of reduced competition in maintaining communities and driving diversification (Case and Taper 2000, Schluter 2000, Chase and Leibold 2003), there are also many instances of surprising similarity between coexisting species, for example among members of functional groups or ecological guilds. In addition, organisms sometimes find nearly identical solutions to evolutionary challenges and converge upon the same ecological niche. Explanations for why competing species might be more similar, rather than different, have gained attention in recent years but continue to be thought of as exceptions to the 'rule' of competitive exclusion (e.g. Wilson 2011). As Abrams (1996) pointed out, although outcomes besides divergence have repeatedly been proposed, there has not been "a correspondingly large number of attempts to find evidence that such nondivergent forms of displacement actually occur."

There remains a consensus that species should be continually pushed to diverge, with occasional instances of some convergence or a weakening of niche-based forces. But what if we were to turn the question on its head and ask ourselves: Why aren't species *more* different? What are the forces that result in more similar species clustering together in communities? What evolutionary dynamics result in convergence instead of divergence? This paper will review and synthesize major theories in this field, and review some of the available evidence in support of these ideas. Chesson's (2000) division of equalizing and stabilizing forces is an excellent framework for attempting to organize the mechanisms behind the coexistence of similar competitors (Figure 3.1, see also Wilson 2011). For example, as Adler et al. (2007) point out, strict neutral theory is a situation with no stabilizing forces, only equalizing ones. And yet, there are some cases where

stabilizing forces may still result in the coexistence of similar species, as we will see below. I will further organize this review by considering ecological and evolutionary mechanisms separately.

How similar *are* co-occurring species?

What do we mean when we claim that co-occurring species are more similar than we would expect? What are the documented patterns that surprise us? If communities are assembled by competitive interactions, we would expect to find evidence of limiting similarity: single species occupying widely spaced positions along niche axes (MacArthur and Levins 1967, May 1974, Roughgarden 1979). Yet in many cases researchers have documented patterns of 'clumping', or 'lumpiness': clusters of species in niche space, instead of regular spacing (Holling 1992, Siemann and Brown 1999, Havlicek and Carpernter 2001).

The idea that communities structured by competition should have fewer co-occurring congeners goes back at least as far as Darwin (1859). And despite vigorous debate over the appropriate null models (Simberloff 1970, Gotelli 2000), the prediction that closely related species are less likely to coexist than more distantly related taxa, still dominates. However, there is a great deal of evidence for *lower* phylogenetic relatedness than expected (Sedio et al. 2012, Harmon-Threatt and Ackerly 2013, Lanier et al. 2013, Riedingera et al. 2013, for a review see Vamosi et al 2009). In some examples, co-occurring species show little or no niche differentiation (Sedio et al. 2012), or trait clustering in addition to phylogenetic similarity (Harmon-Threatt and Ackerly 2013).

A test for character displacement is the comparison of phenotypic divergence between allopatric and sympatric conditions. When species occur in sympatry, character displacement results in higher divergence relative to allopatry. But in several documented

cases, the pattern is reversed and species are found to be *more* similar in sympatry, indicating some form of convergence (e.g. Spaeth 2009). Finally, in contrast to the argument that species cannot occupy the same niche, there have been at least a few documented cases where it appears they do (Blossy 1995, Siepielski et al. 2010, Smith and Leibold. *in prep*.).

Molecular tools have revealed that many taxa, once thought to consist of a single species, are in fact collections of morphologically indistinct species (Witt and Hebert 2000, Colborn *et al*. 2001, Hebert *et al*. 2004, Saez and Lozano 2005). These so-called "cryptic species", which are reproductively isolated from each other yet phenotypically and ecologically indistinguishable (Bickford et al. 2007), appear to be a common phenomenon in many taxonomic groups and biogeographic regions (Pfenninger and Schwenk 2007), yet we still know very little about their ecology. There is increasing recognition that cryptic species are common and important components of biological diversity (Knowlton 1993, Saez and Lozano 2005). Cryptic species do not always overlap in their distributions but when they do their high similarity poses an intriguing challenge to ecological and evolutionary theory (Sàez and Lozano 2005).

ECOLOGICAL MECHANISMS THAT PROMOTE SPECIES SIMILARITY

Habitat filtering

Dating back at least to the origins of the word 'niche' in ecology, we have long recognized the importance of species' environmental requirements in determining where and when they may be found (Grinnell 1917). All environments impose some degree of selection on their occupants, setting the limits of which species may persist locally and filtering out those that cannot from the regional pool of species available to colonize a given site. Consequently local assemblages of species will have broadly similar

requirements resulting in less variation among individuals than a random assemblage sampled from the regional pool (Cornwell and Ackerly 2009). As particular environments prevent the establishment of suitable species, we should expect local communities to share traits such as morphology, life history, and physiology (Grime 2006). The strength and direction of filtering, and thus the degree of trait convergence and the particular suite of traits affected, may vary through time and space, for example along successional stages (Raevel et al. 2012, Purschke et al. 2013). Metacommunity theory describes this kind of habitat selection as species sorting, when species will persist in local communities that match their particular niche requirements (Holyoak et al. 2005), and indeed species sorting may be the most common of the metacommunity paradigms (Cottenie 2005). It is important to remember that while abiotic filters (i.e. those arising from local environmental conditions) may impose some degree of uniformity on the traits of co-occurring species, they are likely to diverge in other sets of traits, thereby promoting the stability of their coexistence (Grime 2006). Nonetheless, studies have found stronger effects of filtering relative to competitive interactions as inferred from phylogenetic and trait distributions (e.g. Uriarte et al. 2010, Sedio et al. 2012). While the balance of clustering or overdispersion may depend on scale (O'Dwyer et al. 2012), a survey of studies examining the phylogenetic structure of communities revealed that clustering (rather than overdispersion or random assembly) is the most commonly observed pattern (Vamosi et al. 2009). Although the precise interpretation of community phylogenetic signals remains problematic (Webb et al. 2002, McPeek 2007, Emerson and Gillespie 2008), the field generally assumes that phylogenetic relatedness can be used as a proxy for ecological similarity, and this assumption has some empirical support from both observational and experimental studies (Ricklefs and Latham 1992, Warren et al. 2008, Burns and Strauss 2011, but see Losos 2008).

'Apparent' filtering

In addition to the filtering of species imposed by the local abiotic environment, there are other mechanisms that may also result in higher similarity of coexisting species. Instead of competing for shared resources, species may instead share predators and in doing so they can engage in "apparent competition" (Holt 1977). Leibold (1998) used a set of models to demonstrate how competition for shared resources, competition via shared enemies (apparent competition), or a combination of both (keystone predation) should result in communities composed of species with more similar requirements (described as zero-net-growth isoclines, or ZNGIs). Contrastingly, species' coexistence in all these models is also favored when they differ in their 'impact vectors', or the manner in which they influence their environments. These impact vectors are in some ways analogous to MacArthur's (1972) 'relative utilization functions' and are directly linked to the per-capita effects species have on their own abundance, and that of their competitors. Thus, this body of theory is generally consistent with much of ecological niche theory – requiring that species differ in their relative impacts in order to coexist stably – while also suggesting we should not be surprised to find high similarity for certain traits (Leibold 1998).

Emergent Neutrality

In models where species compete for shared resources, competitive exclusion will inevitably win out, in the absence of other effects. However, the time it takes for competitive exclusion to play out may be very long, and in fact, should be longer for species that are more similar. In the limit, under strictly neutral conditions, species' abundances will drift. It is worth remembering that when species go extinct via drift, it is not the consequence of an inevitable march towards extinction: their loss will not depend on their degree of similarity with any of their competitors (Aarssen 1983). Given the lack

of realisms and restrictions of such a scenario, it might be fruitful to consider what the distribution of phenotypes is likely to be *during* the process of competitive exclusion under non-neutral conditions.

Scheffer and van Nes (2006) used a model based on classical Lotka-Volterra competition theory to predict the emergence of groups of similar species. While competition does tend to eventually eliminate all but a single niche occupant, with the total number of niches determined by the niche breadth modeled, the transient behavior of their model shows that large numbers of highly similar species can persist for hundreds of generations (Scheffer and van Nes 2006). Similarly, Siepielski et al. (2010) proposed a model of keystone predation in which two different functional groups may coexist via niche differences, with ongoing neutral drift of similar species within each functional group. Scheffer and van Nes (2006) also present a modified version of their competition model, which adds in an extra density-dependence term to increase the strength of intraspecific competition. This stabilizes the transient behavior and the final prediction is that communities should comprise self-organized clusters of species within a series of distinct niches. While Scheffer and van Nes (2006) argue that their 'mild' density-dependence term may arise as a consequence of top-down control by natural enemies, this is just a niche difference in all but name (although some would disagree, see McPeek 2012), which undercuts somewhat their claim of 'emergent neutrality'. Later extensions of this model have also predicted realistic Species Abundance Distributions (SADs, Vergnon et al. 2012) and Species Area Relationships (SARs, Fort and Inchausti 2012).

In addition to their reliance on niche differences to stabilize their model, several authors have argued that the results from these models are particularly sensitive to deviations from Gaussian niche distributions (Herna´ndez-Garci´a et al. 2009, Pigolotti et al. 2007). The form of the competition interaction, which is shaped by the overlap of the

niche distributions, will determine whether lumpy or uniform trait distributions emerge (Pigolotti et al. 2010). There is no doubt that some of the curves used in these models are just as unrealistic as normal Gaussian distributions and it will take careful work to actually measure competition curves before we can settle this issue.

Spatial processes

In their treatment of the mechanisms by which species with similar niches might coexist, Shmida and Ellner (1984) emphasized the role of spatial effects, although they explicitly consider 'trophically equivalent' species, which may still differ in 'life-form, reproductive strategy, and seed-dispersal mechanism'. They describe several effects, including patch dynamics, mass effects, and 'equal chance' (i.e. neutral) dynamics, which can slow down competitive exclusion, potentially allowing trophic niche-equivalent species to coexist (Shmida and Ellner 1984). Refinements of their verbal models and evidence supporting the importance of spatial mechanisms have been greatly developed in recent decades (see Holyoak et al. 2005) although much of this work has focused on space as a resource itself and the ways in which it can be partitioned successfully by coexisting species.

Using a totally different modeling framework – with variable patches, frequent disturbance, and global dispersal – Ernebjerg and Kishony (2011) found that by adding noise to the environmental conditions resulted in the formation of discrete groups of abundant species, clustered along a continuous phenotypic axis. They even suggest that a multidimensional version of their model would predict the emergence of temporary guilds, containing species that share several ecological properties. Another approach that also yields a multimodal species distribution in niche space is that of Lampert and Tlusty (2013). Using a model with a trade-off between maximal growth rate and competitive

ability, they provide an example of how asymmetric competition (as opposed to the symmetrical conditions of the emergent neutrality models) can result in a clumped distribution of trait values.

The ways in which we abstract natural systems – which parts we simplify and how – clearly have a large impact on our predictions. Might the standard lattice grid itself be problematic? Taking into account all the grid cells that are closer to a given individual, rather than just the grid cell it occupies, provides a more realistic description of how resources are partitioned (Liao et al. 2013). This improvement in realism has the added effect of increasing species richness under certain conditions, suggesting that traditional lattice models may overestimate extinction rates (Liao et al. 2013).

In smaller communities, stochasticity will be a more important influence on community outcomes than deterministic competition differences, akin to the effect of small population size on increasing the role of drift in population genetics (Orrock and Fletcher 2005). So, just by random sampling, we may end up with more ecologically similar species in small communities, although this effect cannot *maintain* diversity of similar competitors, since they will easily be lost due to stochastic extinction in small communities.

Over-compensation

Another route to the stable coexistence of two competitors, with identical growth rates, carrying capacities, and competition coefficients, is if species differ in the type of density regulation they undergo, as long as one of them exhibits over-compensation (Münkemüller et al. 2009). This response, in which population size fluctuates wildly around the carrying capacity, so population sizes necessarily must be quite large to avoid stochastic extinctions (Münkemüller et al. 2009).

Reproductive strategy

Chesson (1991) highlighted that if species are capable of distinguishing conspecifics from heterospecifics, then they could coexist without ecological differences, as long as there is a socially-based advantage to aggregation, which in turn would increase intraspecific competition relative to interspecific competition. An example of this was subsequently demonstrated by Zhang et al. (2004), who used a model based on the reproductive behavior of fig-pollinating wasps. Local mate competition and inbreeding in this system leads to a strong female-biased sex ratio, which can be adjusted by ovipositing foundresses. They found that either by responding to the number of conspecific foundresses or the total number of foundresses, two species could stably coexist on a single host. Zhang et al. (2004) argue this effect might help explain the observation that fig species appear to commonly support more than one (often cryptic) wasp species.

An extension of Zhang et al.'s model (2004) has recently been proposed by Montero-Pau and Serra (2011). Inspired by the numerous organisms that exhibit cyclical parthenogenesis, in which species alternate between sexual and asexual strategies, their model starts with Lotka-Volterra competition but includes a density-dependent investment in sex. As one species transitions to invest in sexual reproduction, an opportunity arises for a second species to invade, thereby stabilizing their coexistence as long as their sexual investment strategies differ (Montero-Pau and Serra 2011).

Individual variation

Ecology has a long history of ignoring – or at least averaging over – differences among individuals within species, and instead focusing on modeling dynamics based on mean traits and total population sizes. This is changing as ecologists are beginning to ask

whether and how individual variation affects the outcome of competition and other interactions (Bolnick et al. 2011, Violle et al. 2011).

As described above, habitat filtering will tend to make the constituent species of any local community more similar to one another than a random assortment from the regional species pool. Intriguingly, Jung et al. (2010) point out that individual variation within species will tend to promote species coexistence, by allowing more species to pass through local biotic filters and further, by allowing species to space out along available niche axes in response to competition. Although this will not result in the local coexistence of highly similar, strongly competing species per say, it may be a mechanism promoting higher local species diversity – which, unless one is carefully measuring trait distributions, may be an alternative mechanism for high levels of local species diversity.

Using Lotka-Volterra equations for two competing species, Begon and Wall (1987) demonstrated that by incorporating variation among individuals in competitive ability they could rescue the inferior competitor from competitive exclusion. Their model maintains a consistent distribution of variation across generations and is not inherited, meaning it corresponds to environmentally-induced variation among individuals. More recent approaches that incorporate heritable differences among conspecifics demonstrate the same fundamental concept: that individual variation may enhance coexistence of species that compete for shared resources.

More recently, Vellend (2006) took a similar approach, adding variation among genotypes, and applied it to a both a Lotka-Volterra competition model for more than 2 species and a spatially explicit lattice model of competition. The highest levels of species richness were obtained under low 'niche breadth' (the range over which an individual genotype competes) and high 'potential genotypic range' (the total range over which a species' niche extends). Lichstein et al. (2007) present a model of competition between

two species and show that while intraspecific variation can blur the distinction between competitors and result in neutral-type dynamics, this is only the case when either densities are low or when there is a mean-variance performance trade-off, i.e. inferior competitors have a higher degree of individual variation.

Compiling many decades of detailed growth rate data in forest plots reveals that on average there are many strong positive correlations in growth rates between species, i.e. species respond similarly to change in the environment such as unusually wet or warm years Clark (2010). This similarity is puzzling until one examines the distribution of correlations between growth rates of individuals of different species (i.e. the average of the correlations instead of the correlation of the averages) which turns out to be much lower, and lower even than the correlations between conspecific pairs. This means that the strength of intraspecific competition is indeed higher than interspecific competition. In this way, individual variation helps stabilize coexistence among competing species that – on average – appear to occupy much the same niche (Clark 2010). This mechanism is both simpler and broader in applicability than the enemy-based mechanism invoked by Scheffer and van Nes (2006).

EVOLUTIONARY MECHANISMS THAT PROMOTE SPECIES SIMILARITY

If the traits underlying interactions between species have a heritable portion, then resource competition may result in phenotypic changes over time. The most obvious evolutionary outcome of resource competition is character displacement, in which species limit each other's ability to evolve towards a peak in resource distribution and they end up both with mean phenotypes displaced from the values expected when only a single species is present (Brown and Wilson 1956, Schluter 2001). The relative importance that character displacement in shaping species' phenotypes has been debated but there are a

growing number of well-documented examples where it has played a major role (Schluter 2000). Character displacement may also play an important role in the formation of new species via ecological speciation (Schluter 2000, Pfennig and Pfennig 2005). Nonetheless, character displacement is only one of several different evolutionary responses to resource competition. Below I discuss alternatives and speciation mechanisms that result in the formation of ecological equivalents.

Convergent evolution

Instead of selecting for divergence, there are several scenarios in which competition for shared resources among species will ultimately lead to phenotypic convergence. It is important to note that even early models of character displacement predict convergence, depending on the conditions (Slatkin 1980, Taper and Case 1985). For example, when the range of available niches is small, limiting opportunities for divergence (Taper and Case 1985).

If we consider the types of resources for which species may compete, we may distinguish between substitutable and non-substitutable resources. Substitutable resources might be exchanged for one another, while non-substitutable ones may not (Leon and Tumpson 1975). Abrams (1987) argued that while it is perfectly reasonable to expect divergence under competition for substitutable resources (since species may adaptively shift from one to another without penalty), the expectation under competition for non-substitutable resources is the opposite: species should be expected to converge on similar resource acquisition traits. Essentially, adaptation will favor co-limitation, which in turn selects for convergence (Abrams 1987). Fox and Vasseur (2008) have subsequently shown that under competition for non-substitutable (or what they call 'essential') resources the degree of similarity achieved will depend on differences in resource

requirements. Along the spectrum from substitutable to non-substitutable, resources may be considered 'complementary' (Tilman 1982). Recent modeling work by Vasseur and Fox (2011) demonstrates that when resources are complimentary several outcomes may manifest: convergence, divergence, and parallel shifts in resource use. They also demonstrate that the cost of consuming non-limiting resources, in an effort to maintain a balanced nutritional intake, also imposes selection for trait convergence (Vasseur and Fox 2011).

More recently, TerHorst et al. (2010) modeled the coevolution of species competing for substitutable resources. Although they make several simplifying assumptions, they show that while two species will predictably diverge in resource use, when three or more species are considered they observe both divergence and convergence, and the emergence of clusters of ecologically equivalent species (TerHorst et al. 2010).

Under what other conditions might we expect convergent evolution of species' niches? In 1983, Hubbell and Foster proposed a verbal model for the 'diffuse coevolution' of species traits. Their suggestion (based on ideas previously laid out by Connell 1980) was that species in diverse communities are likely to encounter a wider variety of competitor species than they would in species-poor assemblages. They argued that the selection imposed by this wide range of competitors would put selective pressure on species in multiple directions, rather than in a constant, uniform manner. Thus species should converge on generalist life-history traits over evolutionary time (Hubbell and Foster 1983). Later, Hubbell (2006) proposed an explicit model for the evolution of neutrality, in which he combined levels of spatial heterogeneity, competition for space, and a 20-loci, 2-allele model of trait evolution. The model does not entirely capture the sole effect of 'diffuse coevolution' as described above, as it relies on fine-grained spatial

heterogeneity to generate selective pressure, however, it does predict the evolution of generalists.

There have been several studies aimed not at the evolution of community-wide neutrality, but instead at explaining the clustering of species along niche axes. For example, Bonsall et al.'s (2004) modeling work shows how ecological and evolutionary dynamics can interact to generate patterns in which there are a limited number of ecological niches, but a diversity of highly similar species competing for dominance within each niche. This diversity is transient, but can persist for long time periods. In a model of parasitoids and their hosts, including life-history trade-offs among the parasitoids, Bonsall et al. (2004) predict the evolution of distinct clusters of species along the trade-off niche axis.

Harkening back to the studies of individual variation described above, Yamauchi and Miki (2009) showed that genetic diversity within species promoted coexistence under fluctuating environmental conditions in both a model with sexual reproduction and multiple loci as well as in a model of asexual reproduction and phenotypic plasticity. Alternatively we can think about the role evolution might play, even when the competitors themselves are not the ones undergoing adaptation. In a model of apparent competition between two prey species, Schreiber et al. (2011) demonstrate that the introduction of heritable genetic variability in the predator population makes it much easier to achieve coexistence of both prey species.

Local adaptation

There are several ways in which evolutionary change may contribute to strengthening equalizing forces among species, thereby promoting the coexistence of ecologically similar competitors. Lankau (2011) summarizes how evolutionary change

may "make species more or less equal" via several mechanisms. For example, local adaptation within a heterogeneous landscape may also result in stronger equalizing forces without necessarily invoking convergent evolution of niche positions. Regardless of their ecological niche, when competitively inferior species benefit more from local adaptation than competitive dominants, then their coexistence is promoted (Lankau 2011). Although it is unclear under what exact conditions this may occur. Since inferior competitors often have smaller, more isolated populations, they may benefit from a lack of maladaptive gene flow. However, they are also likely to have lower levels of standing genetic variation for selection to act upon, and will be subject to stronger effects of genetic drift, both of which will limit their ability for effective local adaptation (Lankau 2011).

Mimicry

The evolution of mimicry has famously been described as "a most powerful proof of the theory of natural selection" (Bates 1862) and it by definition suggests that co-occurring species should be phenotypically similar. The evolution of mimicry takes two main forms, Batesian and Mullerian, both of which involve convergent evolution. Under Batesian mimicry, an edible species evolves to match the conspicuous phenotype of a locally co-occurring model species, thereby escaping predation. In Mullerian mimicry several co-mimics all converge on a similar aposematic phenotype, in order to more rapidly teach their predators to avoid them (for a review see Ruxton et al. 2004). Interestingly, competition among mimics has been implicated as a possible candidate for why many cases of mimicry are imperfect, since their strong competitive interactions may in turn foster character displacement (Pfennig and Kikuchi 2012).

Selection for competitive ability

There is a distinction to be made between the ecological niche of a species and its competitive ability. While competitive ability surely stems partially from one's niche – and importantly, how much it overlaps with those of other species – it is possible for two species to occupy the same niche but differ in their competitive abilities (Aarssen 1983). This is often invoked as the reason why inferior competitors are forced to seek out alternative niches (i.e. differentiate) or suffer competitive exclusion. If it is possible for species' competitive abilities to evolve, without adjusting their niche, then there should be strong selection on inferior competitors to improve, while there should be weak to nonexistent selection pressure on competitive dominants. This should result in ongoing coevolution between competitors in a kind of competitive arms race (Aarssen 1983).

Sexual selection

By reducing the extent of range overlap, sexual selection has been suggested as a potential mechanism that may stabilize coexistence (Payne and Krakauer 1997). In a model combining spatial heterogeneity in local carrying capacity and a cost to mate-searching, coexistence is indeed promoted (M'Gonigle et al. 2012). Although not totally stabilized, so the coexistence remains transitory, the model demonstrates that multiple species will persist for several thousand generations without any niche differences between them (M'Gonigle et al. 2012).

Non-ecological speciation

Ecologically equivalent species may be the outcome of convergent evolution, or other selective forces, or they may arise during the process of speciation itself. When a single lineage divides in two, it is not necessarily the case that the resulting sister species are ecologically divergent from one another. While speciation can result in new species

that are ecologically different from their progenitors or from each other (Losos 1990, Schluter 1994), some speciation mechanisms can instead yield species that are similar or nearly identical in their ecology and morphology. For example, if evolution of mate recognition (e.g. Ritchie 2007) or genital morphology (e.g. Stoks et al. 2005) were to occur, there is no requirement that such changes be accompanied by ecological shifts as well. Allopatric speciation may also result in parallel evolution without generating any ecological differences between the new species (McPeek and Gomulkiewicz 2005). Instead, they may continue to share the same probabilities of birth and death, and occupy the same ecological niche and morphological space.

DISCUSSION

There are, it appears, an abundance of mechanisms that may promote the coexistence of similar species (Figure 3.1). To what degree are these mechanisms likely to be operating in natural populations? For some, such as individual variation and spatial processes, there is abundant evidence that the potential certainly exists (i.e. good evidence that individuals differ quite a lot within populations and that they are capable of dispersing among populations in meaningful quantities); yet we still lack a complete theoretical understanding of their influence on coexistence. For examples like habitat filtering, I would argue that there is both a solid theoretical framework in place, and good evidence that it plays an important role in structuring competitive communities. And for some forces, including local adaptation, convergent evolution, and emergent neutrality, we lack both a complete understanding of their predicted effects on coexistence and some measure of their importance relative to diversifying pressures.

As with so many disciplines, perhaps one way forward is to consider the joint effects of some of the above-described mechanisms in order to better understand how

likely they are to ultimately influence community structure. For example, if we start with Scheffer and van Nes' (2006) emergent neutrality model (but without their density-dependence term), but extend their framework to a 2-patch model with dispersal in both directions, we observe the same formation of transient clumps. However, the rate at which species go extinct from the simulations slows down with dispersal (Figure 3.2). The time until the first extinction is longer with dispersal, and the total number of species still present at the end of 2000 generations is higher.

Begon and Wall's (1987) demonstration that individual variation stabilizes competitive coexistence of two species can be extended to a three-species model, and the effect still holds (Figure 3.3). If we start with a model of convergent evolution (TerHorst et al. 2010) and combine it with some level of individual variation, we find that the eventual survival of all three species is more likely (Figure 3.4). These examples demonstrate the inferential power gained from combining approaches.

Ghilarov (1984) argued that perhaps the importance of convergence "has caught so little attention [because there] is a constant desire to find everywhere divergence." That convergence and parallel evolution have continued to be neglected, relative to the emphasis placed on character displacement and competitive exclusion, may speak to the continuing bias among biologists to preoccupy themselves with explanations of diversity, rather than similarity. Vadas (1990) claimed that convergence was likely to be "common, in spite of the dogma [of character divergence]", but that we lack evidence "because the topic has not met with widespread interest by field ecologists." I would counter that community ecology has shown remarkable flexibility as a discipline in recent years (Gravel et al. 2006, Adler et al. 2007, Leibold and McPeek 2006) and we can expect that a real synthesis of theory for diversity and similarity is not far off.

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FIGURES

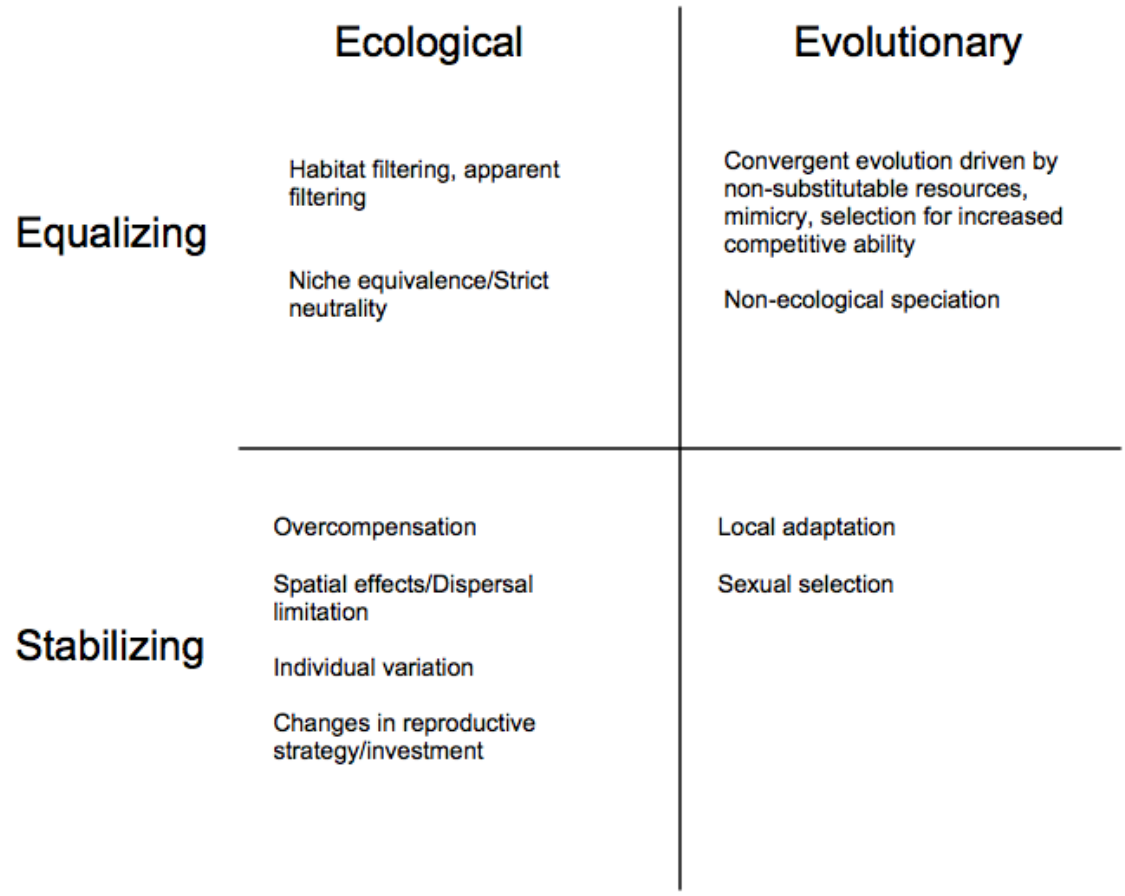

Figure 3.1. Schematic illustrating the ecological and evolutionary forces that promote the co-occurrence of similar species.

Sections are divided using Chesson's (2000) terminology of equalizing and stabilizing forces.

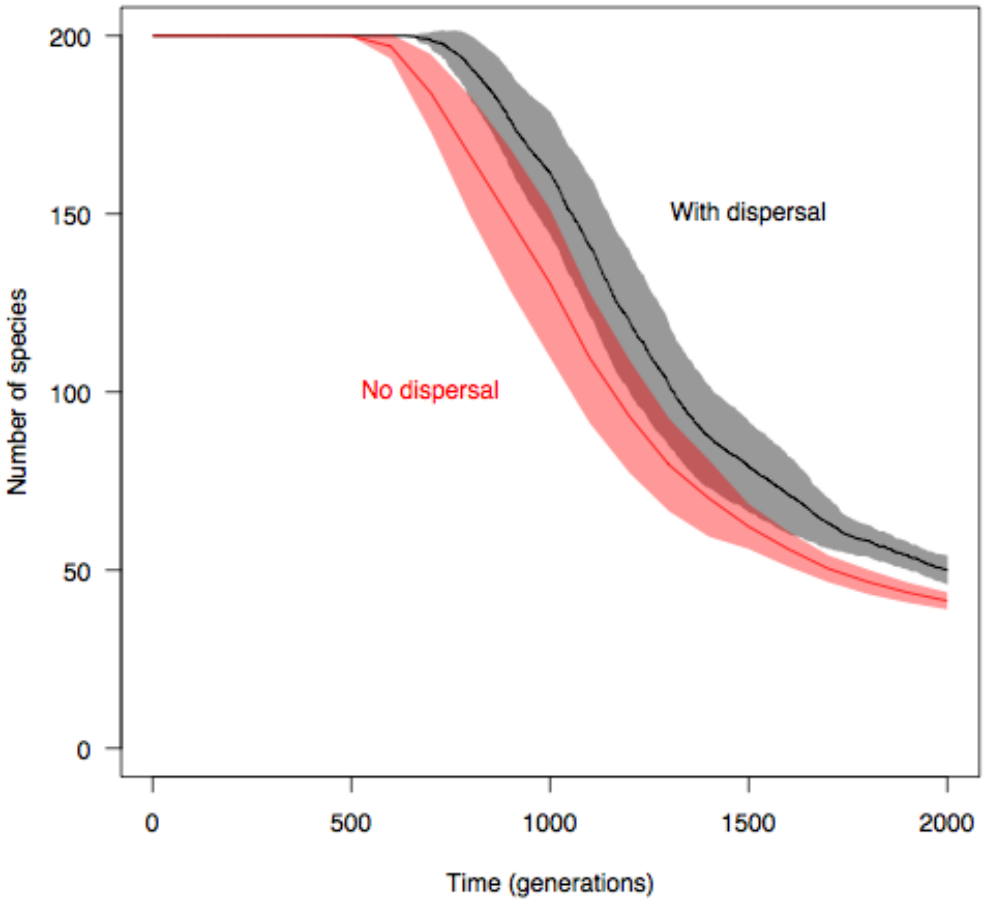

Figure 3.2. Effects of combining a two-patch dispersal model with Scheffer and van Nes' (2006) emergent neutrality model.

In both cases there is a precipitous drop in the number of species after approximately 500 generations. The decline starts later when there is dispersal and the number of coexisting species is higher at the end of 2000 generations. Solid lines represent the average of 20 model runs and the shading corresponds to 95% confidence intervals. As in Scheffer and van Nes' (2006) original model, we modeled population growth with a Lotka-Volterra competition equation,

$$\frac{dN_i}{dt} = rN_i\left(K_i - \sum_j \alpha_{i,j}N_j\right)\Big/K_i \quad i = 1,2,\ldots n$$

where N is the biomass of a given species i, r is the maximum per capita growth rate, K is the carrying capacity for that same species I, and $a_{i,j}$ is the competition coefficient term that scales the effect of species j on species i. The effect of a species on itself is set to 1. The competition coefficients between species were calculated for each pair of species by measuring the overlap of their niche distributions,

$$\alpha_{ij} = e^{-\frac{(\mu_i - \mu_j)^2}{4\sigma^2}}$$

Where the μ values correspond to the mean niche position of each species, and σ sets the width of the niche distribution .To avoid border effects, I imposed periodic boundary conditions so that each species has equal numbers of competitors on both sides by taking the minimal distance between $|\mu_i - \mu_j|$ and $1 - |\mu_i - \mu_j|$ (Fort et al. 2009). Following Scheffer and van Nes (2006), communities were initialized with 200 species, each set to an initial abundance of 0.1 and a mean niche position drawn from a random uniform distribution, ranging from 0 to 1 and the standard deviation for each niche distribution was set to 0.15. For the runs where I incorporated dispersal, I tracked the abundance of each species in two patches and allowed a random percentage (from a uniform distribution between 0 and 5%) to migrate from one patch to the other in each generation.

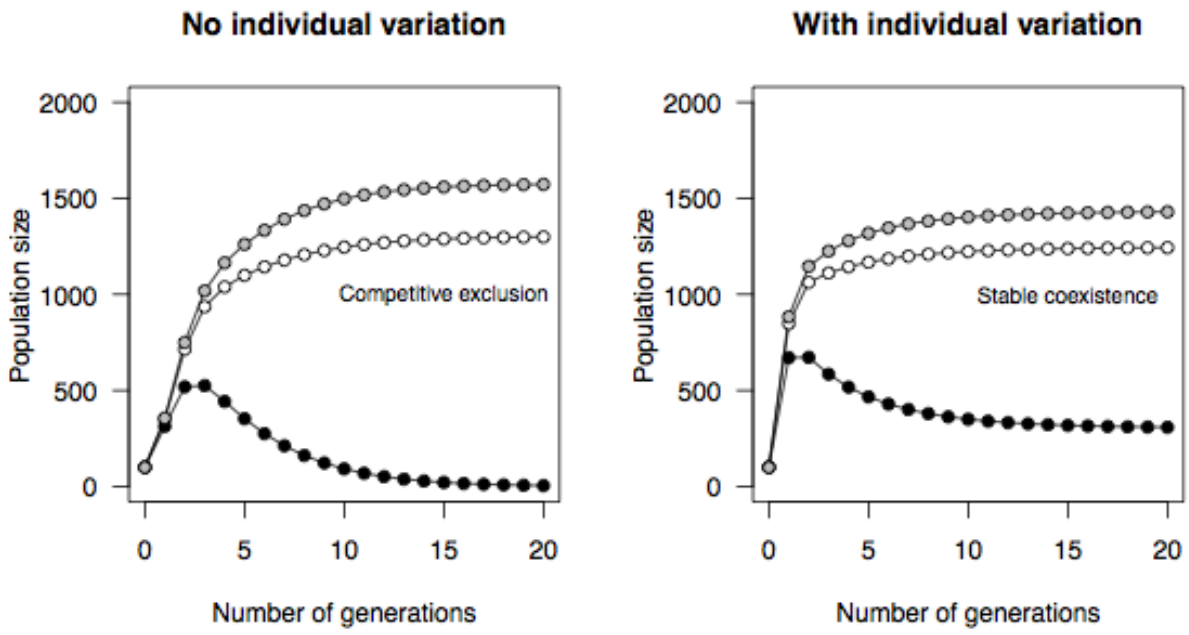

Figure 3.3. The stabilizing effect of individual variation.

Modifying Begon and Wall's (1987) 2-species model to include 3 species demonstrates that the stabilizing effect of individual variation extends to larger numbers of competing species. Begon and Wall (1987) use the following version of the Lotka-Volterra competition equation (slightly modified):

$$N_{i,t+1} = \frac{N_{i,t}R_i}{1+\left(\frac{(R_i-1)(\alpha_{ii}N_i+\alpha_{ij}N_j)}{K_i}\right)}$$

Then they incorporate a fixed set of proportions (0.065, 0.125, 0.1875, 0.25, 0.1875, 0.125, and 0.065) for assigning individuals slightly varying values for both their competition coefficients and their carrying capacities. In the above figure I have modified only the competition coefficients for the three competing species.

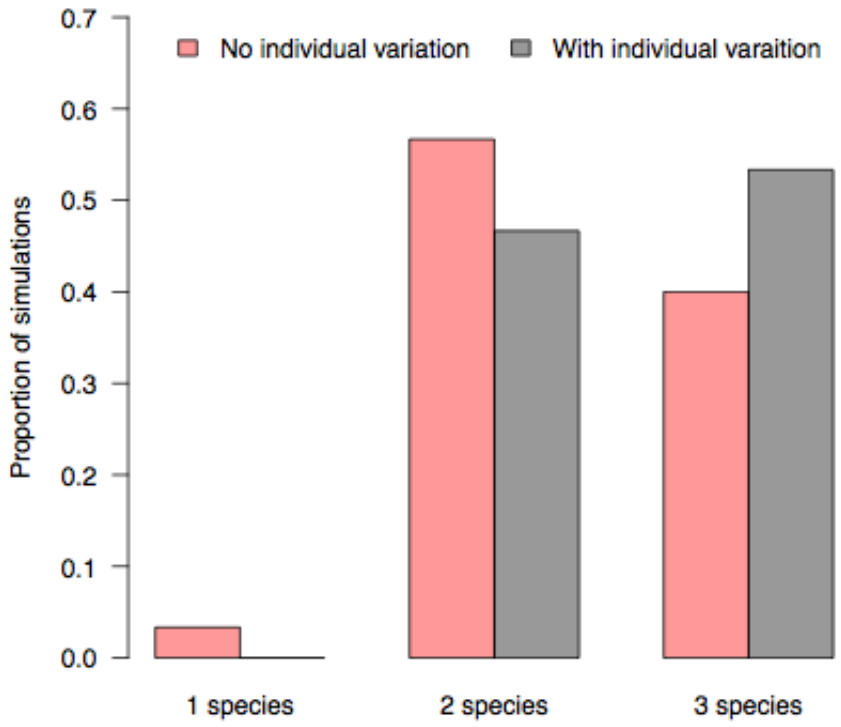

Figure 3.4. The effect of individual variation on a model of evolutionary convergence.

When individual variation is incorporated into TerHorst et al.'s (2010) model we find it much more likely to have all three species survive and coexist. TerHorst et al. (2010) use a formula from Levins (1968) to calculate the competition coefficients for three species consuming two resources, **A**,

$$\mathbf{A} = \mathbf{W}\mathbf{U}t(\mathbf{U})$$

where **W** is a vector of niche widths, and **U** represents a matrix of resource use. In their model of trait evolution a small mutation of the resource use matrix occurs in each time step, allowing uptake of a given resource to increase or decrease, and

the most fit type immediately goes to fixation before the next generation. I modified their model to further incorporate individual variation, as implemented by Begon and Wall (1987). As in Begon and Wall (1987), since the variation itself is not inherited, it is thought to represent the kind of heterogeneity that arises via environmental heterogeneity.

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